Is This Hand for Real? Attenuation of the Rubber Hand Illusion by Transcranial Magnetic Stimulation over the Inferior Parietal Lobule

Marjolein P. M. Kammers[1], Lennart Verhagen[1,2], H. Chris Dijkerman[1], Hinze Hogendoorn[1], Frederique De Vignemont[3], and Dennis J. L. G. Schutter[1]

Abstract

■ In the rubber hand illusion (RHI), participants incorporate a rubber hand into a mental representation of one's body. This deceptive feeling of ownership is accompanied by recalibration of the perceived position of the participant's real hand toward the rubber hand. Neuroimaging data suggest involvement of the posterior parietal lobule during induction of the RHI, when recalibration of the real hand toward the rubber hand takes place. Here, we used off-line low-frequency repetitive transcranial magnetic stimulation (rTMS) in a double-blind, sham-controlled within-subjects design to investigate the role of the inferior posterior parietal lobule (IPL) in establishing the RHI directly. Results showed that rTMS over the IPL attenuated the strength of the RHI for immediate perceptual body judgments only. In contrast, delayed perceptual responses were unaffected. Furthermore, ballistic action responses as well as subjective self-reports of feeling of ownership over the rubber hand remained unaffected by rTMS over the IPL. These findings are in line with previous research showing that the RHI can be broken down into dissociable bodily sensations. The illusion does not merely affect the embodiment of the rubber hand but also influences the experience and localization of one's own hand in an independent manner. Finally, the present findings concur with a multicomponent model of somatosensory body representations, wherein the IPL plays a pivotal role in subserving perceptual body judgments, but not actions or higher-order affective bodily judgments. ■

INTRODUCTION

Synchronous stroking of one's own occluded hand and an anatomically congruent, visible rubber hand leads to feeling of ownership over the rubber hand. This illusion is known as the rubber hand illusion (RHI). The RHI has been interpreted as the temporary incorporation of the rubber hand into the participant's mental body representation and is generally measured through perceptual judgments about the relocation of the participants' limb toward the rubber hand, or through self-reports in which participants subjectively rate the degree to which they experience a feeling of ownership over the rubber hand. Interestingly however, in case of a multisensory mismatch between tactile and visual information, or in case of an incongruent spatial configuration of the rubber hand, there is no feeling of ownership over the rubber hand, nor any relocation of the participant's own hand (Durgin, Evans, Dunphy, Klostermann, & Simmons, 2007; Ehrsson, Holmes, & Passingham, 2005; Tsakiris & Haggard, 2005; Ehrsson, Spence, & Passingham, 2004; Botvinick & Cohen, 1998).

A recent principal component analysis showed that feeling of ownership is not a single perceptual experience, but that bodily self-consciousness can be decomposed into different components (Longo, Schuur, Kammers, Tsakiris, & Haggard, 2008). Four major components of bodily sensations have been identified with subjective self-reports: (1) *embodiment* of the rubber hand, (2) *loss of one's own hand*, (3) *movement*, and (4) *affect*. Additionally, for the *embodiment* component, the following subcomponents could be distinguished: (i) *ownership* over the rubber hand, (ii) *location*, and (iii) *agency*. The *ownership* subcomponent concerns statements about the sensation that the rubber hand belongs to one's own body, whereas the *location* subcomponent comprises statements concerning the experience that the rubber hand and one's own hand occupy the same location in space. These two subcomponents are, independently of each other, significant predictors of the degree of relocation of the own hand toward the rubber hand as measured with a perceptual location judgment. Consequently, there seems to be a dissociation between the degree to which the rubber hand feels like part of one's body, and the perceived (re)location of one's body. More recently, we showed

[1]Utrecht University, Utrecht, The Netherlands, [2]Radboud University, Nijmegen, The Netherlands, [3]Institut Jean-Nicod, Paris, France

that relocation of a participant's own hand is task dependent. Whereas perceptual location judgments are sensitive to the RHI, ballistic actions with or toward the illuded stimulated hand resist the RHI (Kammers, De Vignemont, Verhagen, & Dijkerman, 2008).

Several studies have looked into the neural correlates of feeling of ownership (Tsakiris, Hesse, Boy, Haggard, & Fink, 2007; Ehrsson et al., 2004, 2005; Botvinick, 2004). Most recently, the involvement of the right posterior insula and the frontal operculum in the RHI was demonstrated using positron emission tomography (Tsakiris et al., 2007). A functional magnetic resonance imaging study showed a significant relationship between bilateral ventral premotor activity and subjective ratings of ownership over the rubber hand during the RHI (Ehrsson et al., 2004). Additionally, enhanced inferior parietal lobule (IPL) activity was observed during induction of the RHI, that is, when recalibration of the perceived position of one's own limb is taking place (Ehrsson et al., 2004, 2005). This pattern of activation suggests that activity in ventral premotor areas and the IPL might correspond to the feeling of *ownership* over the rubber hand and *location* of one's own hand subcomponents, respectively, as identified in the study of Longo et al. (2008).

Although there is no clear consensus on the possible network of cortical areas subserving the different components of the RHI, the IPL seems a likely candidate for involvement in the relocation of the participant's own limb. In favor of this hypothesis, it was shown that the IPL plays a pivotal role in maintaining spatial relationships of body parts as evidenced by patients with autotopagnosia (Buxbaum & Coslett, 2001; Sirigu, Grafman, Bressler, & Sunderland, 1991). Furthermore, Dijkerman and de Haan (2007) proposed a theoretical model for cortical somatosensory processing, in which the IPL is thought to be important in processing information for perceptual body judgments, such as judgments about the spatial body configuration and metric properties (Dijkerman & de Haan, 2007). This aspect of the model has not yet been tested directly, and the direct involvement of the IPL in the RHI has not yet been demonstrated.

In the current study, we applied off-line low-frequency repetitive transcranial magnetic stimulation (rTMS) over the inferior posterior parietal lobule (IPL) to investigate the involvement of this area in the generation of the RHI dependent perceived relocation of one's own hand toward the rubber hand. Participants reported the felt position of their stimulated right hand both immediately after induction of the RHI, as well as after making two reach-to-point movements. In addition, subjective ratings of feeling of ownership were obtained by conducting a standard RHI questionnaire (Botvinick & Cohen, 1998).

Based on the existing correlational evidence that suggests IPL involvement in the generation of the RHI (Ehrsson et al., 2004), our main hypothesis was that rTMS-related inhibition of activity of the IPL contralateral to the stimulated hand would reduce the strength of the illusion as measured by the perceptual relocation of the own hand toward the rubber hand (the location subcomponent of the RHI). Notably, because the IPL has not been implicated in the ownership subcomponent of embodiment of the rubber hand, we did not expect IPL involvement in the subjective ratings of feeling of ownership. Furthermore, based on our previous finding that the RHI primarily affects perceptual judgments (Kammers et al., 2008), we hypothesized the reach-to-point movements themselves to be robust against the RHI, and thus, to remain unaffected by rTMS over the IPL. The final aim of our study was to investigate the effect updated proprioceptive information due to active movements might have on the strength of the illusion measured by a subsequent perceptual judgment in combination with rTMS over the IPL.

METHODS

Participants

Fourteen healthy nonsmoking volunteers (9 women) participated in the study. One participant was excluded due to failure to return for the second session. All participants were aged between 18 and 25 years (mean ± *SD* = 22.2 ± 2.4 years), were right-handed, and all women used oral contraceptives. None of the participants had a history of psychiatric or neurological conditions and all had normal or corrected-to-normal vision. Written informed consent was obtained and volunteers were paid for participation. The study was approved by the medical ethical committee of the Utrecht University in accordance with the Declaration of Helsinki. All volunteers were naïve to the rationale of the experiment.

Experimental Design and Procedure

In a double-blind, sham-controlled, counterbalanced crossover design, participants received either 20 min of "real" or sham 1 Hz rTMS (1200 pulses) in two consecutive sessions. Upon arrival at the laboratory, participants were screened for contraindications to TMS (Keel, Smith, & Wassermann, 2000), and received oral and written information on the experiment. Informed consent was obtained and right handedness was assessed with the Dutch Handedness Inventory (inclusion criteria score of >7), mean score ± *SD* = 9.92 ± 0.28 (Van Strien, 1992). Next, resting motor threshold (MT) of the left hemisphere was determined according to the standardized procedure as described by Schutter and van Honk (2006) (mean ± *SD* = 49.7 ± 12.7% of maximum stimulator output; Schutter & van Honk, 2006). Finally, an appointment for the first testing session was made.

At the start of each of the two testing sessions, either sham or real low-frequency rTMS was applied to the left

IPL by Experimenter 1. After rTMS, the second experimenter entered and collected the behavioral data in a total of 20 trials. Both the participant and the second experimenter were unaware of the type of rTMS stimulation. Each trial started with 60 sec of RHI induction, which could either be synchronous (illusion condition) or asynchronous (control condition). Next, a perceptual response was recorded, followed by two action responses and, finally, a second perceptual response (please see Figure 1 for a schematic representation of the procedure). Each of the two action responses could be carried out with either the stimulated right hand or the nonstimulated left hand, such that there were four possible combinations for the action responses on a given trial. Action response combinations with the same hand (i.e., twice with left or twice with right) were recorded six times, whereas action response combinations involving both hands (i.e., with right and, subsequently, with left, or vice versa) were recorded four times. The 20 trials were divided in half, and after each half, a questionnaire was conducted such that the participant completed the same questionnaire twice, once for the control condition and once for the illusion condition.

Rubber Hand Illusion

Participants were placed behind a framework in which the two forearms were placed. The participant's stimulated right side was occluded from vision throughout the experiment. During the induction phase, participants could see a right rubber hand and their own left forearm. Participants' own occluded right index finger and the right index finger of the visible rubber hand were stroked either synchronously (illusion condition) or asynchronously (control condition) for 60 sec in an unpredictable manner with a mean rate of approximately 1 Hz. After induction, participants were asked to close their eyes, and a board was lowered to occlude all hands (real right and left hand, as well as the rubber hand) from vision. Next, the responses were collected.

First Perceptual Response

The first perceptual response was collected directly after induction and prior to any action response by the participant. Participants verbally indicated when the experimenter's index fingers mirrored the perceived locations of their own stimulated right and nonstimulated left index fingers. The experimenter placed both his index fingers on top of the board occluding the participant's hands, which could be done either at the center of the board or at the outside edges. Subsequently, the experimenter started moving both index fingers either outward or inward, respectively. The sliding movement along the edge of the board was at an unpredictable pace and at a different speed for each finger, as well as between trials, in order to prevent carryover effects between trials. Participants were free to verbally instruct

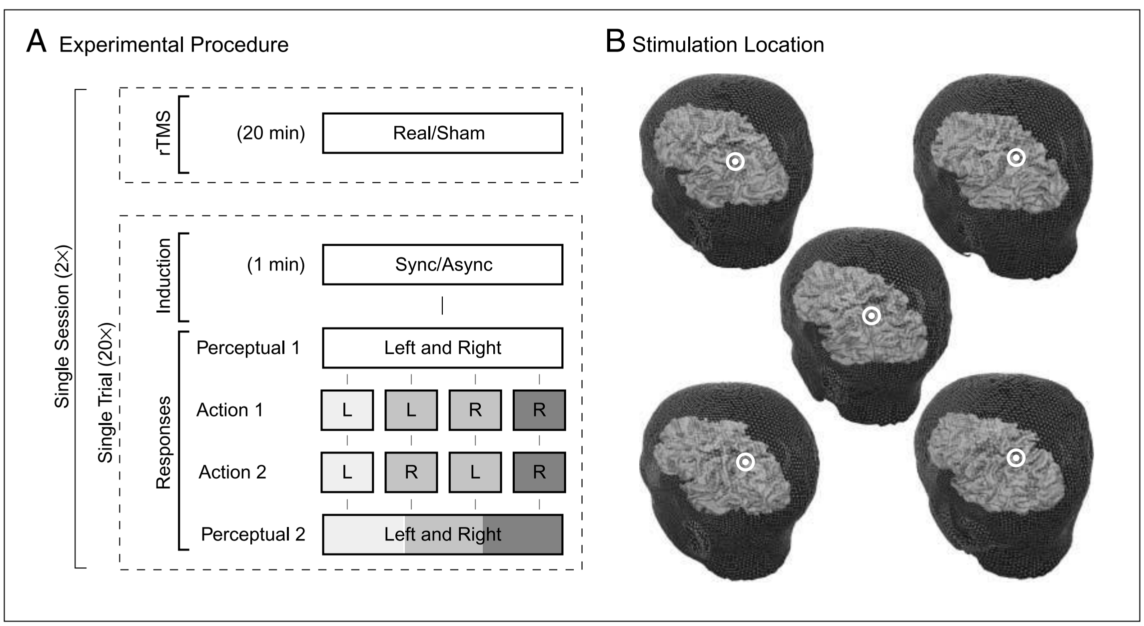

Figure 1. Experimental procedure and rTMS location. (A) The experimental procedure consisted of two sessions, divided on the level of rTMS. Each session started with 20 min of either real or sham rTMS, followed by 20 behavioral trials. Each behavioral trial was made up of 1 min of RHI induction followed by a perceptual response, two action responses, and finally, a second perceptual response. (B) The stimulation localization of rTMS of five subjects. The targets indicate respective locations of EEG cap electrode TP3.

the experimenter to move his index fingers until they thought that they mirrored the felt location of their own unseen index fingers. Finally, the experimenter calculated the difference score between the indicated and veridical location for each finger separately on a ruler placed outside the visual field of the participant, which formed the endpoint error. This type of perceptual response allowed for recording of the nonstimulated left hand as well as the stimulated right hand simultaneously, without increasing the chance of the participant giving standardized responses.

The strength of the RHI was calculated by subtracting the endpoint error for each index finger in the control condition (asynchronous stroking) from the illusion condition (synchronous stroking).

Action Responses

Next, two ballistic reach-to-point actions were made in each trial, in one of four different combinations. Actions could be executed with the nonstimulated left hand as well as with the stimulated right hand, whereby the goal of the actions always consisted of the index finger of the other hand. The four different movement combinations were: (1) reaching twice with the index finger of the nonstimulated left hand; (2) reaching first with the nonstimulated left hand, followed by reaching with the stimulated right hand; (3) reaching first with the stimulated right hand, followed by reaching with the nonstimulated left hand; and (4) reaching twice with the stimulated right hand.

The various combinations of action responses provided different proprioceptive update about the location of the participant's right hand. Because localization of our body parts relies heavily on proprioceptive information, we expected that the different action response combinations would have differential effects on the subsequent perceptual response. Specifically, we anticipated that new proprioceptive update from movements of the illuded right hand would reduce the perceived relocation of the stimulated right hand, whereas moving the nonilluded left hand would not. As a result, the strength of the illusion would be maximal following two responses with the left hand, intermediate following one response with each hand, and minimal following two responses with the right hand. Because there was no difference in updated proprioceptive information between movement combinations using each hand once (2 and 3), we did not expect to find a difference between these conditions. In order to prevent direct contact between the two hands, a board was placed above the target hand on which the reaching hand landed to indicate the perceived location of the index finger directly underneath. Finally, the participant replaced his hand to its starting position, which was indicated by a small patch of Velcro.

Second Perceptual Response(s)

Finally, in the second perceptual response phase, the first perceptual response was repeated. The second perceptual response was analyzed separately for each of the four action response combinations preceding the perceptual location judgment, in order to evaluate the effect of progressive proprioceptive update on the subsequent perceptual response.

Questionnaire

Participants were asked to complete a questionnaire in which they rated nine questions concerning possible sensations related to the rubber hand. The questionnaire was based on those developed by Ehrsson et al. (2005) and Botvinick and Cohen (1998). The questionnaire was completed a total of four times: once after an illusion trial (synchronous stroking) and once after a control trial (asynchronous stroking), for both the real and sham rTMS testing session.

Kinematic Parameters

All movements were recorded using an electromagnetic movement recording system (Minibird, Ascension Technologies) sampling the positions of the tips of the index fingers at 100 Hz.

The dependent variable of interest was the absolute endpoint error, that is, the distance between indicated and veridical positions of the tip of the target index finger at movement offset, along the axis parallel to the movement. This is a direct measure of relocation of the participant's own hand. Other investigated kinematic parameters were: reaction time (the time between the verbal instruction and the onset of the movement), movement time (the time between movement onset and movement offset), peak velocity (the maximum velocity during movement time), relative time to peak velocity (the time from movement onset to peak velocity relative to the movement time), and trajectory distance (the total Euclidean distance traveled by the index finger during the movement time). Together these parameters give an indication of, and are sensitive to, disturbances of both the motor plan and the execution of the movement (Jeannerod, 1984).

Kinematic data were sampled continuously and low-pass filtered (fourth-order Butterworth filter at 10 Hz), after which the velocity of the two markers was calculated. To keep the visual information constant, a dummy marker was attached to the index finger of the rubber hand. The onset of the movement was determined when velocity exceeded 0.1 m/sec, for over 0.6 sec. In other words, the movement onset was determined as the first time point for which the subsequent 6 time points all have a velocity exceeding 0.1 m/sec. The offset of the movement was set to the moment the velocity remained below 0.1 m/sec for over 0.2 sec. Hence, the offset was determined as the first time point for which the following 2 time points were below 0.1 m/sec. Using these strict parameters, two valid movements (one forward to the perceived target and one back to the starting position) were detected in all trials for all participants.

Transcranial Magnetic Stimulation

Off-line low-frequency rTMS was performed using a biphasic magnetic brain stimulator (maximum output 4160 A peak/1750 VAC peak) with an eight-shaped iron core coil (Neotonus, Atlanta).

Low-frequency rTMS has shown to selectively reduce cortical excitability that outlasts the initial block of stimulation creating a window for studying its behavioral effects (Hallett, 2007; Robertson, Théoret, & Pascual-Leone, 2003).

Although TMS has shown to provide different effects on cortical excitability (i.e., inhibitory as well as facilitatory) (Silvanto & Muggleton, 2008), the general idea behind the reductions in cortical excitability is that low-frequency rTMS at intensities below the MT predominantly acts on activating GABA interneurons in the superficial layers of the cerebral cortex, subsequently causing a local transient state of reduced cortical excitability (Daskalakis, Fitzgerald, & Christensen, 2007). For example, in a recent study, it was shown that in comparison to applying low-frequency rTMS over the primary motor cortex, low-frequency rTMS over the posterior parietal cortex impaired oculomotor control (Hutton & Weekes, 2007). Others have demonstrated in a placebo-controlled study that 20 min of low-frequency rTMS at 90% MT over the parietal, but not occipital, cortex impairs top–down spatial processing (Aleman et al., 2002). Together, these studies demonstrate that off-line rTMS is a useful perturbation method to investigate cortical brain functions in humans (Robertson et al., 2003).

Sham rTMS was performed using a modified but visually identical coil, which had an aluminum plate built in the housing directly under the iron core (Neotonus, Atlanta). The sham coil mimics the sound click and sensation of real TMS, but the brain is shielded from actual stimulation, and as consequence, this constituted the control condition.

Participants received 20 min of either real or sham 1-Hz rTMS, applied to the left inferior posterior parietal lobule at 80% MT (1200 pulses). This was done in two repeated sessions, which were separated by at least 24 hr. The order of sessions was counterbalanced across participants. The left IPL was targeted, according to the International 10–20 EEG System, by marking the TP3 electrode site using an EEG cap (Jasper, 1958). It should be noted that the left IPL was targeted because the illusion was induced on the contralateral right side. Stimulation parameters were in line with the safety guidelines of the International Federation of Clinical Neurophysiology (www.ifcn.info).

Notably, a complete testing session took an average of 70 min, and never took longer than 90 min, including the 20 min of rTMS stimulation. Although exact chronometric information on the effects of 20 min off-line low-frequency rTMS to the left parietal cortex is not available, off-line low-frequency rTMS with similar frequency and duration applied to the anterior cortical regions induced changes in electric brain activity that remained detectable 60 min after stimulation (Schutter, van Honk, d'Alfonso, Postma, & de Haan, 2001). Providing the evidence that there is considerable overlap between the effects of TMS on cortical physiology across the cerebral cortex (e.g., Daskalakis et al., 2008; Deblieck, Thompson, Iacoboni, & Wu, 2008), it is reasonable to assume that 20 min of off-line low-frequency rTMS creates a time window that is sufficiently long enough to investigate the functional relationship between the left inferior parietal cortex and the RHI.

Structural Scans

Structural MRI scans were obtained using a Siemens Avanto 1.5-T MRI scanner (whole brain 1 × 1 × 1 mm resolution, T1 weighted), for a subset of participants after completion of the study to verify that the IPL was, in fact, being stimulated.

The stimulated location was marked using a vitamin pill placed on the EEG cap. Three-dimensional renders of participants' left hemispheres were created using the BrainVoyager software package (Brain Innovation, Maastricht, The Netherlands). Post hoc inspection of the stimulated location verified that the inferior posterior parietal lobule had been targeted as intended.

RESULTS

TMS was well tolerated by all participants and no adverse events occurred.

First Perceptual Response

A 2 × 2 repeated measures analysis of variance was conducted on the relocation error of the participant's stimulated own right hand, with the factors TMS (sham vs. real) and RHI (control vs. illusion) for the first perceptual response. Most importantly, the two-way interaction between TMS and RHI was significant [$F(1, 12) = 5.86$, $p = .032$]. Post hoc paired-samples t tests showed that rTMS significantly reduced the strength of the illusion in the illusion condition [$t(12) = 4.77$, $p < .001$; mean error toward the rubber hand ± *SEM*: real rTMS = 11.04 ± 0.80; sham = 12.72 ± 0.77; Figure 2, leftmost bars]. No effect of rTMS was found for the first perceptual response in the control RHI condition [$t(12) = -0.41$,

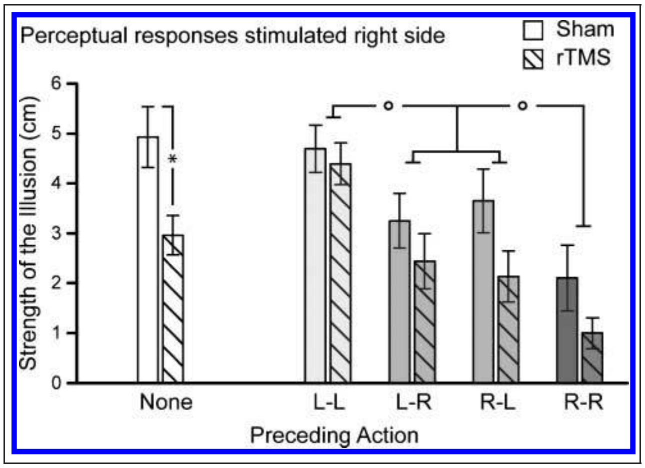

Figure 2. Effect of rTMS on the perceptual response. (A) Illusion strength (illusion–control) for perceptual responses for the stimulated right hand. Data columns represent mean values for all participants (13). Open and hashed bars indicate responses after sham and real rTMS, respectively. Dark and light bars indicate the type of preceding actions. The asterisk indicates the significant attenuation of the strength of the illusion after real rTMS compared to sham. The circles indicate the gradual attenuation of the effect of the RHI for the second perceptual responses, depending on the type of preceding action. Error bars represent standard errors of the mean.

$p = .69$; mean error toward the rubber hand ± *SEM*: real rTMS = 8.07 ± 0.91; sham = 7.78 ± 1.10].

There was also a main effect of RHI [$F(1, 12) = 167.07$, $p < .0001$], indicating a larger error toward the rubber hand after synchronous stroking.

Action Responses

There was no main effect of rTMS or RHI for the endpoint errors for the different reach-to-point movements, supporting our earlier finding that the RHI predominantly affects perceptual judgments rather than motor judgments (Kammers et al., 2008). There was also no significant interaction between rTMS and the endpoint errors. Other kinematic parameters for the first reaching response were analyzed in a 2 × 2 × 2 repeated measures analysis of variance with the factors rTMS (real vs. sham), RHI (control vs. illusion), and hand (stimulated right vs. nonstimulated left). The factor hand was included in the analysis because action responses of both hands serve as a measure of possible relocation of the right hand, either as the target (pointing with the nonstimulated left hand toward the stimulated right hand) or as the means (pointing with the stimulated right hand). This is in contradiction to the perceptual judgment, where the localization of the left hand is unrelated to the perceived location of the stimulated right hand.

There were several significant effects for the other four kinematic parameters: a main effect of hand on movement time [$F(1, 12) = 5.53$, $p = .037$; Stimulated right > Nonstimulated left], peak velocity [$F(1, 12) = 7.35$, $p = .019$; Nonstimulated left > Stimulated right], and relative time-to-peak velocity [$F(1, 12) = 7.68$, $p = .017$; Stimulated right > Nonstimulated left]. There was also a main effect of RHI on movement time [$F(1, 12) = 5.07$, $p = .044$; Illusion > Control]. Finally, there was a significant two-way interaction between rTMS and Hand on reaction time [$F(1, 12) = 9.25$, $p = .010$; Illuded right × rTMS > Others]. Hence, no main effect of rTMS was observed. Most importantly, the critical three-way interaction (rTMS × RHI × Hand) did not reach significance for any of the kinematic parameters (all p values ≥ .074).

Importantly, it should be noted that effects on the kinematic variables are weak in general. When adjusting for the multiple comparisons on the four kinematic parameters by applying a Bonferroni correction, the alpha level is reduced to a value of .0125. This more conservative approach would lead to only a significant two-way rTMS × Hand for reaction time.

In short, ballistic reaching movements with the right stimulated hand were slower and reached peak velocity later than pointing movements with the nonstimulated left hand. Furthermore, a significant interaction was observed for reaction time, between hand and rTMS, showing an effect of rTMS for the right hand that was independent of the RHI. In other words, independent of a relocation of the right hand as a consequence of synchronous multisensory stimulation.

Overall, the difference in kinematic parameters between both hands can likely be ascribed to hand preference, or indicate a certain degree of uncertainty of the initial starting position of the right hand as a result of the lack of visual information of this hand throughout the experiment.

Analyses for the second reaching responses showed no significant effects for rTMS.

Second Perceptual Responses

Relocation errors, that is, the strength of the illusion, for the second perceptual responses were entered into a 2 × 2 × 4 repeated measures analysis of variance, with the factors rTMS, RHI, and response. The factor response divided trials on the basis of which hand(s) the participant had used to make the two preceding reach-to-point movements: (1) twice left, (2) left then right, (3) right then left, or (4) twice right. We found a significant main effect of RHI [$F(1, 12) = 140.03$, $p < .0001$], showing a larger relocation error toward the rubber hand after synchronous stroking (i.e., for the illusion condition). There was no main effect of rTMS [$F(1, 12) = 0.81$, $p = .39$], indicating no difference between sham and real rTMS. There was, however, a significant main effect of response [$F(3, 12) = 30.02$, $p < .0001$]: The largest relocation error was observed when there was no proprioceptive update of the stimulated right hand (4). The two-way RHI × Response interaction was also significant [$F(3, 12) = 18.75$, $p < .0001$]. Post hoc paired-sample *t* tests showed that the strength of the RHI was greatest when the second perceptual response was preceded by no movement of the stimulated right hand (1), and smallest when the perceptual response was preceded by two movements with the stimulated right hand (please see Figure 2, rightmost bars). Crucially, none of the interactions with rTMS were significant (all p values > .161).

Questionnaire

A MANOVA for the nine questions with the factors rTMS (sham vs. real) and RHI (control vs. illusion) showed a significant main effect of RHI for the three illusion-related questions only: (Q1) It seemed as if I was feeling the touch at the location where I saw the rubber hand being touched [$F(1, 12) = 13.14, p < .001$]; (Q2) It seemed as though the touch I felt was caused by the stimulation on the rubber hand [$F(1, 12) = 39.17, p <$ .000]; and (Q3) I felt as if the rubber hand was my own hand [$F(1, 12) = 11.91, p < .001$]. No other significant effects were observed (all p values < .89).

DISCUSSION

The present study investigated the role of the left inferior posterior parietal lobule (IPL) in perceptual body representations by modifying its cortical excitability with off-line low-frequency rTMS. We observed that the RHI was reduced for immediate but not for delayed perceptual responses. This selective effect of rTMS on the relocation component of the RHI suggests that: (1) the IPL is directly involved in immediate perceptual (re)localization of our limbs during induction of the RHI but is, nonetheless, not necessary for eventual RHI-dependent relocation of the stimulated limb; (2) the IPL does not directly subserve ballistic actions; and (3) the subjective experience of the ownership over the rubber hand is not associated with the IPL.

First, the immediate perceptual response showed attenuation of the RHI for the stimulated right hand only after real rTMS in the illusion condition. This interaction is critical. The absence of an effect of rTMS in the control condition when no RHI was induced suggests that the IPL is directly involved in recalibrating the perceived position of the contralateral limb during the induction of the RHI. This restricted attenuation of the RHI concurs with the findings of Ehrsson et al. (2004), who implicated the IPL during RHI induction. In addition, this notion supports a theoretical model of somatosensory body representations in which the IPL plays a critical role in maintaining metric aspects of the body's spatial configuration (Dijkerman & de Haan, 2007). This model suggests that the perceptual experience of our body is subserved by higher-order processing within the IPL as well as the posterior insula. Whereas the insula is considered to be involved in affective aspects of bodily experience (Craig, 2002) and body ownership (Tsakiris et al., 2007), the IPL is importantly involved in the perception of size and location (Ehrsson et al., 2005). The current findings strengthen so far mainly correlational evidence by reserving a crucial role for the IPL in the modulation of perceptual body experiences. For future research, it would be of great interest to investigate whether modification of cortical excitability in ventral premotor areas might selectively reduce the subjective feeling of ownership without altering the relocation of the stimulated own hand toward the rubber hand. Furthermore, the second perceptual responses showed that the RHI strength is increasingly attenuated as participants made successive movements with the stimulated right hand, thereby receiving proprioceptive update about its veridical position. The integration of new proprioceptive information into the body representation remains unaffected after rTMS. This suggests that the IPL is involved in recalibration of the perceptual location of the own limb, based mainly on visual rather than on proprioceptive input. This is in line with the frequently observed partial recalibration of the participant's own hand toward the rubber hand compared to the often near-complete spatial referral of the sensation of touch and feeling of ownership questions (Lloyd, 2007; Tsakiris & Haggard, 2005; Botvinick & Cohen, 1998). Moreover, it also coincides with the distinction between different body representations (Head & Holmes, 1911–1912), now often reported in the body representation literature. On the one hand, the body schema is thought to underlie ballistic actions, subsequently incorporating the body as a whole, whereby the incoming proprioceptive information might be weighted more heavily than visual information. The body image, on the other hand, is considered mainly to subserve bodily perceptual judgments, and to be more visually guided (Gallagher, 1986, 2005; Paillard, 1991, 1999; Gallagher & Cole, 1995).

Second, although rTMS to the IPL strongly reduced the immediate perceptual response directly after induction, no such rTMS effect was found on the second perceptual response. Following the short delay in which participants made two reach-to-point movements, the illusion was restored to its "original" strength (i.e., identical to RHI strength after sham rTMS). One possible interpretation is that rTMS to the IPL simply causes a systematic *delay* in the construction of the new internal body representation underlying the perceptual RHI response, without completely preventing it. Other examples of time dependence within different components of the RHI have previously been shown by Botvinick and Cohen (1998), who showed enhanced feeling of ownership over the rubber hand after longer induction times (Botvinick & Cohen, 1998). An alternative interpretation of the restored strength of the relocation of the participant's own hand is that the recovery of RHI strength might be due to general motor activity (in which the body is a means to a goal, rather than a target), in which the interaction between motor and perceptual systems allows updating of the body representation normally subserved by the IPL. Further research will be necessary to distinguish between these hypotheses, for instance, by looking into whether inactivity between two perceptual responses is also sufficient to restore the effect of the RHI.

The robustness of the present action response seems to be in contradiction with reported illusion sensitive action responses found, for instance, in a previous RHI experiment (Botvinick & Cohen, 1998). However, actions can differ on several levels, for instance, on the amount of on-line control. The motor program underlying goal-directed action can be fully specified before the movement onset, but also undergo continuous updating during the movement execution, especially during the deceleration phase of the action. Fast ballistic reach-to-point actions are especially apt to be fully prespecified, and are known to be resistant to perceptual visual illusions (Goodale & Milner, 1992). In the RHI study of Botvinick and Cohen (1998), participants performed a slow gliding movement whereby the index finger was in continuous contact with the table surface, and the participants were free to adjust and correct their finger position until satisfied. Such a slow action is more easily subject to on-line control, and more prone to be influenced by visual memory and perceptual information compared to the fast ballistic actions used in the present study. Illusory sensitivity of actions has also been shown in the mirror illusion (Holmes, Snijders, & Spence, 2006). However, in the study of Holmes et al. (2006), although participants could not see their moving hand, they did see the target location. This alone could bias and increase the relevance of continuous visuomotor processing during the movement. In sum, we argue that the actions performed in the present study are ballistic without on-line control and insensitive to (higher-order) perceptual influences, which is in contrast to the on-line control of slow actions.

Although we found strong perceptual behavioral reductions in RHI strength, we did not find any effect of rTMS on subjective ratings of the feeling of ownership over the rubber hand. There was no main effect of rTMS on the questions, nor was there an rTMS $\times$ RHI interaction. In other words, rTMS to the IPL did not significantly alter the subjective experience of the feeling of ownership, and only those questions referring to feeling of ownership-specific experiences showed a difference in the subjective experience between synchronous (illusion) and asynchronous (control) stroking. A possible explanation might be that at the time the questionnaire was conducted, that is, at the end of the trial, the strength of the RHI was restored to its original level and possible effects of rTMS had been eliminated, particularly because the behavioral effects of rTMS are usually very subtle. However, although the present results may not cover the complex interplay between subjective ratings of feeling of ownership over the rubber hand and the more objective perceptual relocation of one's own hand, the selective effect of rTMS is in line with the recently presented dissociation between different RHI components (Longo et al., 2008). Longo et al. (2008) showed that the subjective experience of embodiment during the RHI is not a single perceptual experience, but that it can be broken down into different components. More specifically, the fact that *loss of own hand* is dissociable from *embodiment* of the rubber hand indicates that the RHI does not solely involve the mere additional incorporation of the rubber hand. The effect of the RHI should therefore also be considered in terms of relocated sensations of one's own hand independently of feeling of ownership over the rubber hand. This replaced sensation of one's own hand has been interpreted in terms of a highly dynamic underlying body representation. Possibly, rTMS to the IPL may have affected plasticity of the body representation underlying perceptual location judgments of the participant's own hand. Or rTMS interfered with overwriting the location of one's own hand by the rubber hand. However, it may not affect the higher-order subjective experience of embodiment of the rubber hand itself, which is considered to involve processing in other cortical areas such as the posterior insula and the premotor cortex (Dijkerman & de Haan, 2007; Tsakiris et al., 2007; Ehrsson et al., 2004).

It should furthermore be noted that it is important to test whether the observed behavioral modulation on the first perceptual response of the stimulated right hand could be the result of possible decline of the effect of rTMS over time. Because rTMS reduced the strength of the illusion, if the effect of rTMS declined over the test session, we would expect illusion strength to increase over time. Further analysis of our data shows that there was no order effect. We divided each real rTMS session in two, and compared the strength of the illusion (synchronous–asynchronous) in the first perceptual responses in the first block to those in the second block. There was no significant difference [$t(12) = 0.75, p > .46$] between early trials and late trials, suggesting that the effects of rTMS did not decline as the session progressed.

In addition to the rTMS effect over time, we tested three other important rTMS RHI aspects. First, the two-way interaction for the first perceptual response on the stimulated right hand and the lack of rTMS effect on the action responses showed that the effect of rTMS was only apparent for the illusion condition. In other words, there was only a reduction of the relocation of the stimulated right hand toward the rubber hand after synchronous stroking, that is, when there was ownership over the rubber hand. This addresses two important aspects, namely, the task specificity of rTMS and the illusion specificity of the effect of the rTMS. The third important factor is hemispheric specificity. This can be shown by investigation of the nonstimulated left hand. There was no significant main effect for RHI [$F(1, 12) = 0.15$, $p = .70$] or for rTMS [$F(1, 12) = 0.00$, $p = .99$] on the nonstimulated left hand. This confirms that the effect of the RHI is restricted to the stimulated hand only. These main effects, in combination with the lack of significance of the two-way interaction between RHI and rTMS for the nonstimulated left hand [$F(1, 12) = 0.43$, $p = .52$], show the possible hemispheric specificity of the rTMS modulation of the left IPL. This provides converging evidence that we might have successfully restricted the effect of rTMS to the targeted region. However, we presently did not examine the role of the right IPL in the RHI of the right hand. Because there is ample evidence that the effects of off-line low-frequency rTMS are not restricted to the circumscribed location and involve remote areas including the contralateral side, future research addressing the hemispheric contributions to the RHI is warranted.

In conclusion, this study replicates our previous finding that the RHI mainly affects the perceptual, rather than the sensorimotor, representation of the body. This is in line with the idea that body representations subserving actions represent the body in a more holistic and global fashion than body representations underlying perceptual judgments, which are thought to be more local and distinct. Most importantly, we have shown the involvement of IPL in the relocation of one's own limb for immediate perceptual responses, as opposed to actions or delayed perceptual responses, indicating that although the left IPL is critically involved in initiating the RHI, the left IPL is not necessary for the eventual occurrence of the illusion.

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Reprint requests should be sent to Marjolein P. M. Kammers, Helmholtz Institute, Experimental Psychology, Utrecht University, Room 16.24 Van Unnikbuilding, Heidelberglaan 2, 3584 CS Utrecht, The Netherlands, or via e-mail: m.p.m.kammers@uu.nl.

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